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Nitrogen supply – A determinant in water use efficiency of winter wheat grown under free air CO_2 enrichment

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ABSTRACT

Global warming and associated decrease of summer precipitation will intensify the limitation of crop growth through water unavailability in Europe. Concomitantly, the rise of atmospheric CO_2 concentration ($[CO_2]$) decreases stomatal conductance and thus transpiration as evident at the leaf level. However, knowledge about the effect of elevated $[CO_2]$ ($[eCO_2]$) on seasonal water use of crops is rather poor. In a two year field study, winter wheat was grown under ambient $[CO_2]$ (393 ppm) and $[eCO_2]$ (600 ppm) using free air CO_2 enrichment (FACE). In addition, subplots were established with three levels of nitrogen (N) supply (35, 190, 320 kg N ha^{-1}). Soil moisture was continuously measured and wheat was irrigated when necessary to keep field capacity at between 50% to 90%. Evapotranspiration (ET) from stem elongation until maturity was calculated using a soil water balance approach. Water use efficiency (WUE) was determined from the ratio of aboveground biomass production and ET during this period.

Increasing N supply increased canopy size and decreased radiation transmission to the soil surface. Moreover increasing N supply enhanced biomass production from 771–1569 g m^{-2}, ET from 227 to 336 mm and WUE from 4.07 to 6.20 g kg^{-1}. Biomass was increased under $[eCO_2]$ by 17% among all N levels. $[eCO_2]$ increased soil moisture especially in the upper soil layer (0–20 cm) and thus irrigation was reduced under $[eCO_2]$ compared to $[aCO_2]$. This effect was intensified by rising N supply leading to a significant $CO_2 \times N$ interaction on ET and WUE. Thus, the $[eCO_2]$ effect was for ET −2, −9 and −10% and for WUE + 20, + 30 and + 29% under 35, 190, 320 kg N ha^{-1}, respectively. Simultaneously, there seems to be a greater increase of evaporation by $[eCO_2]$ under low than high N supply.

1. Introduction

The anthropogenic rise of the atmospheric CO_2 level and the related consequences for regional changes in temperature and annual precipitation pattern might intensify the water limitation of crop growth during the vegetation period (Porter et al., 2014). Concomitantly, the rising atmospheric CO_2 concentration ($[CO_2]$) increases photosynthesis of C3 crops and reduce stomatal conductance and thus transpiration at the leaf level of C3 and C4 crops (Ainsworth and Rogers, 2007). However, for reliable estimations of the consequences of water shortage on crop growth in future the effect of elevated $[CO_2]$ ($[eCO_2]$) on crop water use under field conditions has to be quantified.

Previous CO_2 enrichment studies with wheat indicated that a rise of $[CO_2]$ of approximately 200 ppm above the ambient $[CO_2]$ decreases stomatal conductance by 30–40% (Bunce, 2004; Wall et al., 2000; Li et al., 2004; Tausz-Posch et al., 2013). Also, stomatal response to $[eCO_2]$ was found to be stronger under low than high nitrogen (N) fertilization (Li et al., 2004; Wall et al., 2000). The reduction of stomatal conductance and transpiration at the leaf level can be counterbalanced by an increase of leaf area under $[eCO_2]$. This has been observed in controlled environment studies under high but not under low N supply (Li et al., 2004; Seneweera and Conroy, 2005). However, if plants were grown in the field under adequate N fertilization, effects of $[eCO_2]$ on leaf area index were small (Brooks et al., 2000; Weigel and Manderscheid, 2012). Water loss from the canopy is strongly influenced by atmospheric conditions including radiation, air humidity and wind speed. Therefore, reliable estimation of the effect of $[eCO_2]$ on canopy transpiration and seasonal water use are ideally possibly if plants are grown under free air CO_2 enrichment (FACE) (Long et al., 2004).

In FACE studies with wheat $[eCO_2]$ decreased canopy transpiration

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by 15% to 22% (Senock et al., 1996; Tausz-Posch et al., 2013) and evapotranspiration (ET) by 4% to 20% (Burkart et al., 2011; Kimball et al., 1995; Hunsaker et al., 2000; O'Leary et al., 2015; Wang et al., 2018). Results for water savings by [eCO_2] under N deficiency are variable indicating ET reductions of 20% and 2% when estimated from an energy balance approach (Kimball et al., 1999) and from a soil water balance (Hunsaker et al., 2000), respectively.

Water use efficiency of biomass production of wheat was clearly stimulated under FACE (Kimball, 2016). The size of the effect of [eCO_2] was almost +20% under optimum growth conditions (Hunsaker et al., 2000). However, results obtained under limited N supply showed either an enlargement or a mitigation of the CO_2 effect as compared to the ample N treatment depending on the method used for measuring ET (Hunsaker et al., 2000; Kimball et al., 1999).

In a wheat field water flux to the atmosphere includes mainly evaporation from the soil and transpiration through the stomata of the plants and less importantly, evaporation of water intercepted by the canopy. Only transpiration is associated with plant productivity whereas evaporation is considered as an undesired component of ET. Evaporation can contribute 10% to 40% to ET in a wheat field (Caviglia and Sadras, 2001; Chen et al., 2010; Kool et al., 2014) and under normal growth conditions average seasonal evaporation amounts to about 30% of ET (Liu et al., 2002). Evaporation is controlled by soil water content of the topsoil and the amount of radiation incident to the soil surface. The latter depends on leaf area index which determines radiation transmitted to the soil surface.

The reduction of transpiration under [eCO_2] can result in an increase of soil water content (Hunsaker et al., 1996; Burkart et al., 2011). Thus, it is possible that water saved by transpiration under [eCO_2] is wasted by an increase of evaporation. Since evaporation is much more facilitated under low than high N supply due to the associated changes in canopy size (Debaeke and Aboudrare, 2004), it is conceivable that an increase of evaporation as a result of a decrease of transpiration under [eCO_2] is more important under low than under high N supply.

In a recent study with different wheat growth models the effect of global warming and [eCO_2] on seasonal transpiration and evaporation was estimated (Cammarano et al., 2016). According to this study, a doubling of [CO_2] hardly decreases seasonal water use and the effect on seasonal evaporation was even stronger (-9%) than on transpiration (-2%). However, there was a great variability among the models regarding the contribution of evaporation to total water use which points to the need of more reliable data for this interaction.

FACE experiments addressing ET of wheat carried out so far were conducted in an arid (Hunsaker et al., 1996, 2000) or a semi-arid environment (O'Leary et al., 2015) using a water balance or an energy balance approach (Kimball et al., 1999). In the only large-scale FACE study done in the temperate climate zone of Central Europe ET was measured with a canopy chamber which, however, altered the aerial environment of the plant (e.g. wind speed; radiation environment) influencing ET (Burkart et al., 2011). Thus, there is a lack of data and knowledge, respectively, with respect to the effect of [eCO_2] on seasonal ET of wheat which is especially true for the temperate climate zone.

The present paper describes the first study that addresses the effects of FACE on ET and water use efficiency of winter wheat over the main growing seasons of two years under temperate climate conditions combined with three N fertilizer levels (severe deficiency, adequate and excess N supply). The main objective was to quantify the effect of [eCO_2] on ET and on water use efficiency and to examine whether the response to [eCO_2] is modified by N fertilization.

2. Materials and methods

2.1. Experimental site and FACE system

The experiment was conducted on a field site (52°18'N, 10°26'E, 79 m a.s.l.) at the Thünen-Institute in Braunschweig, Germany, in 2014 and 2015. The mean annual temperature is 9.1 °C and the mean annual precipitation is 617 mm.The soil is a luvisol of a loamy sand texture (69% sand, 24% silt, 7% clay) in the plough horizon (0–40 cm). The soil profile has a depth of about 60 cm (−30 cm Ap, −15 cm Al, −15 cm Bt, > 60–70 cm CII). The lower layers are almost pure sand. Overall, the soil is of low to intermediate fertility and provides a comparatively shallow rooting zone.

CO_2 enrichment was carried out by a FACE system constructed according to the Brookhaven National Laboratory design (Lewin et al., 1992). Three circular plots were equipped each with a free air CO_2 enrichment apparatus including vertical vent pipes and CO_2 injection driven by a blower and each with a diameter of 20 m. This rings comprised what is termed [eCO_2] treatment. Three further circular plots without the CO_2 enrichment apparatus were used as control treatment (=[aCO_2]). The FACE and ambient rings were set up after crop emergence and removed at grain maturity. The target CO_2 concentration in the FACE rings was set to 600 ppm. The CO_2 enrichment lasted from the three leaf stage in March until end of grain filling in July (Table 1). CO_2 enrichment took place during the daytime hours and was interrupted if wind speed exceeded 6 m s^{-1} or if air temperature fell below 5 °C.

Climate data (hourly/daily mean values of air temperature, global radiation and precipitation) measured at 2 m height close to the experimental field site (< 500 m) were provided by the German Weather Service at Braunschweig

2.2. Crop management

Winter wheat (*Triticum aestivum* L. variety "Batis") was sown at the experimental field site in late autumn with a density of 380 kernels m^{-2} (Table 1). Crop management measures were performed according to local farm practice with adequate nutrient supply and pesticide applications.

In each of the FACE and ambient rings three subplots (3 m × 5 m) with different N fertilization were randomly established. The N treatments comprised three levels of calcium ammonium nitrate (deficient: N1, adequate: N2, excessive: N3). The total amount of N fertilizer applied in the two years were 40/35 kg N ha^{-1} (N1), 180/200 kg N ha^{-1} (N2) and 320 kg N ha^{-1} (N3). A detailed description of the different N treatments is described elsewhere (Dier et al., 2018).

2.3. Measurement of soil water content and seasonal water use

According to a previous study with the same wheat cultivar at this site the greatest part of roots is in the 0–30 cm topsoil layer (Pacholsky et al., 2015). Thus, soil water content (SWC) was measured in the 0-0.2 m and 0.2-0.4 m soil layer by time domain reflectometry (TDR, from

Table 1
Important cultivation measures and growth stages.

Event	2014	2015
Sowing	Oct 29th	Nov 4th
Emergence	Nov 18th	Nov 19th
Start CO_2 enrichment	Mar 31th	Mar 12th
1st node stage	Apr 18th	Apr 30th
First Harvesting	Apr 24th	May 4th
Anthesis	June 6th	June 12th
End of CO_2 enrichment	July 21th	July 24th
Final harvest	July 22th	July 27th

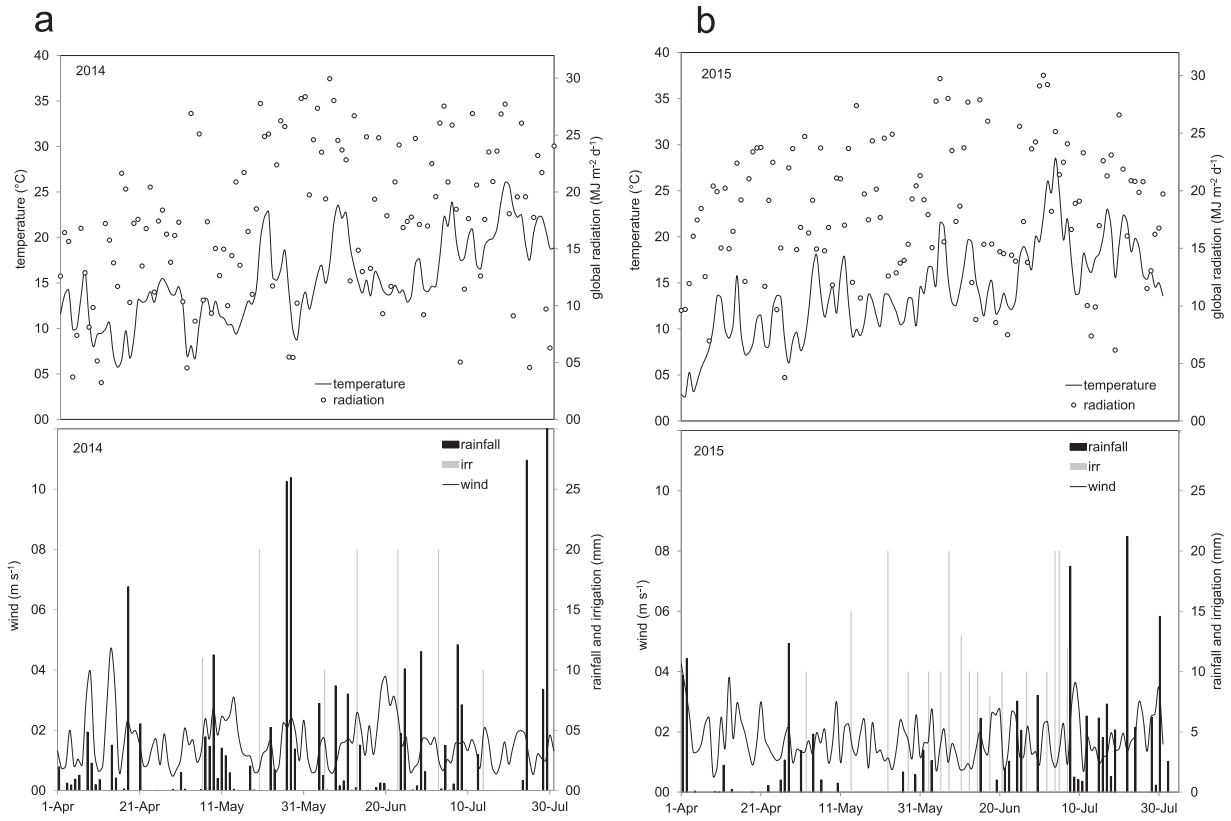

Fig. 1. Daily means of air temperature, global radiation, wind speed (at 2 m in height), and daily sum of rainfall and irrigation during the main growing period in 2014 (a) and 2015 (b). Daily irrigation quantity (irr) is shown for the [aCO_2] treatment with excessive N supply (N3).

IMKO, Ettlingen, Germany). Measurements were done approximately twice per week during the main growing period and in all 18 replicates of the different CO_2 and N treatments. The drained upper and lower limits of plant available volumetric soil water content were 23% and 5%, respectively. The average of SWC in the 0-0.4 m soil profile was used to control water availability and plant water use.

It was intended to keep the SWC within the range of 50% and 90% of field capacity by irrigation to prevent drought and nitrate leaching. This was achieved by modelling the soil water budget with the AMBAV model (Kersebaum et al., 2005), which was done by the Agrometeorological Research Station of the German Weather service at Braunschweig. The model runs were continuously controlled and re-parameterized if necessary by the regular measurements of SWC obtained by the TDR probes. Irrigation was done with a hand-held shower according to the variable water demand of the treatment plots due to the different N and CO_2 supply.

It was assumed that the soil profile for plant water uptake was restricted to 0-0.4 m. There was no capillary rise to the root zone since ground water level is about 10 m below surface. Furthermore, it was assumed that drainage from the root zone and surface runoff were negligible. Thus, plant water use was calculated using a simple soil water balance:

$$ET = R + I + dW$$

where ET is evapotranspiration, R is rainfall, I is irrigation and dW is water content change in the root zone (0-0.4 m) from stem elongation to maturity. This period lasted from 25th April to 17th July in 2014 and from 4th May to 20 July in 2015, respectively.

2.4. Measurement of light transmission by the green canopy, crop growth and water use efficiency

Fraction of PAR transmitted by the green canopy (f_{trans}) was measured at noon (± 2 h) approximately once per week starting few days before stem elongation. The measurements were carried out with the SUNSCAN system (DeltaT Devices, Cambridge, UK) and included the radiation incident to the canopy (J_0), and the radiation at the lower limit of the green canopy (J_c), which was visually estimated. J_c was measured two to four times in each subplot of the different CO_2 and N treatments. f_{trans} was determined as the ratio of J_c to J_0.

Plants were harvested from an area of 0.5 m^2 and 1.8 m^2 at the beginning of stem elongation and at grain maturity, respectively (Table 1). Plant material was dried at 105 °C until constant weight and total plant dry weight per ground area was calculated.

Water use efficiency was calculated from the ratio of water use between stem elongation and maturity and the production of above ground dry weight during this period.

2.5. Statistical analysis

The experiment was analyzed as split plot design with the CO_2 treatment as main plot factor and the N treatment as sub plot factor and F-tests were conducted with SAS (version 9.4) proc mixed. If the year was included into the analysis, then F-tests were implemented as repeated measurements by using the UN(1) model for the variance/covariance between the years of the random main plot and residual error. The UN(1) model applies no covariance between the years, but allows for different error variances in each year.

3. Results

3.1. Performance of the FACE system and environmental conditions

During the growing seasons, CO_2 enrichment was interrupted for 1.0% of the operational time in 2014 and for 2.6% in 2015 due to high wind speeds. The 1 min average [CO_2] was within the range of

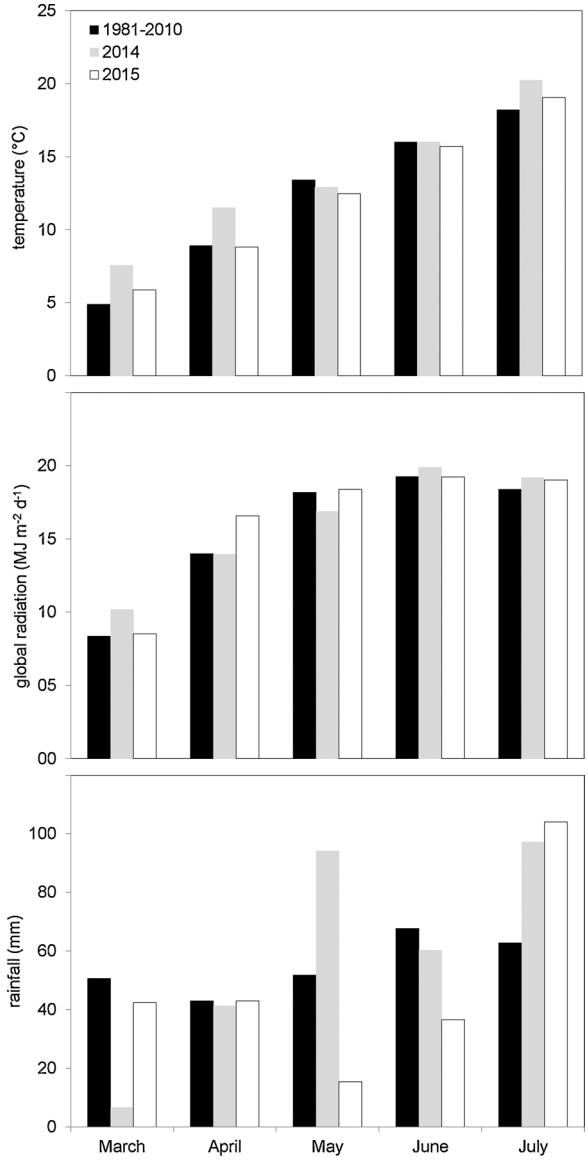

Fig. 2. Monthly long-term mean (1981–2010) and monthly averages in 2014 and 2015 for temperature, global radiation and rainfall.

600 ppm ± 10% for 95.6% and 95.7% for the operation time in 2014 and 2015, respectively. The average daytime [CO_2] at the ambient air plots was 394 ppm in 2014 and 392 ppm in 2015.

Daily values of the weather conditions for the main growing season are shown in Fig. 1. Overall, the weather conditions were within the long-term range of variation of this site with only minor deviations (Fig. 2). In 2014, air temperature was higher in March and April as compared to the long-term mean. In 2015, rainfall from May to June was only half that of the long-term mean.

3.2. Water supply, soil water content and seasonal water use

Rainfall from stem elongation until maturity was 181 mm in 2014 and 122 mm in 2015. Thus, irrigation requirement was much greater in 2015 than 2014 (Table 2). Soil water content (SWC) fluctuated more strongly in 2014 than in 2015 due to the differences in precipitation (Fig. 3). In 2015, more than half of the crop water requirement was met by irrigation that was adjusted on the basis of SWC

In 2014, SWC exceeded field capacity several times in the top soil layer and once in the 0.2-0.4 m soil layer at the end of May during an intensive rainfall of 55 mm over three days (Fig. 1). From mid of May to grain maturity SWC in the topsoil layer was often significantly higher under [eCO_2], although FACE plots received less irrigation than ambient plots (Table 2). There were significant differences in SWC among the N levels in the topsoil layer, whereby SWC decreased with rising N supply. In 2015, SWC exceeded field capacity only at the end of the growing season in the top soil layer. Significant effects of the CO_2 and N treatments on SWC occurred much more rarely in 2015 than in 2014 because of the high share of water supply coming from coordinated irrigation.

Table 2
Timing and amount of irrigation (mm) applied to wheat grown under different CO_2 ([aCO_2], [eCO_2]) and nitrogen supply (deficient, N1; adequate, N2; excessive, N3) during 2014 and 2015. Sum of rain is given since 25th April in 2014 and 5th May in 2015.

date	N1		N2		N3		
	[aCO_2]	[eCO_2]	[aCO_2]	[eCO_2]	[aCO_2]	[eCO_2]	sum of rain
5.5.14	11	11	11	11	11	11	2
20.5.14			20	20	20	20	32
5.6.14			10	10	10	10	103
12.6.14	10	10	20	20	20	20	121
23.6.14			20	15	20	15	126
3.7.14			20	20	20	20	155
14.7.14					10		181
25.4-17.7.14	21	21	101	96	111	96	181
12.5.15	15	15	15	15	15	15	3
21.5.15	20	20	20	20	20	20	4
25.5.15			10	10	10	10	5
30.5.15			10		10		11
2.6.15	10	10			10	10	13
4.6.15	10	10	10	10	10	10	13
5.6.15			10	10	10	10	13
8.6.15	13	13	13	13	13	13	13
10.6.15	5		5		10		13
12.6.15	10	10	10	10	10	10	13
13.6.15	8	8	8	8	8	8	19
18.6.15	10		10		10		22
24.6.15			10	10	10	10	39
29.6.15	5	5	10	10	10	10	47
1.7.15			10	5	20	10	47
2.7.15					10	10	47
3.7.15	10	10	10	10	10	10	47
5.7.15	5	5	10	10	12	10	66
4.5 - 20.7.15	121	106	171	141	208	166	122

Irrigation was increased with rising N supply and decreased in [eCO_2] plots (Table 2). Adjustment of irrigation to the N treatments was started from mid of May in both years and to [eCO_2] at anthesis in 2014 and two weeks before anthesis in 2015. Amounts of irrigation applied to the different N treatments under [aCO_2] ranged from 21 mm to 111 mm in 2014 and from 121 mm to 208 mm in 2015. Plots under [eCO_2] received 15 mm less watering under N deficiency and 42 mm less watering under high N.

Seasonal ET increased with rising N supply from 225 mm at N1 to 309 mm at N3 when averaged over all years and CO_2 treatments (Table 3). The effect of N supply on seasonal ET in the [aCO_2] plots was almost similar between both years. However, in the N2 and N3 treatments the [eCO_2] effect was much stronger in 2015 than in 2014, leading to a significant CO2 x N interaction on ET in 2015 but not in 2014 (Table 4). However, if the year effect was included into the statistical analysis, then there was a significant CO2 x N interaction on ET, but no significant CO2 x N x year interaction. Averaged over both years, the [eCO_2] treatment decreased ET by 2% at low N and by 10% at excessive N (Table 5 and 6).

3.3. Radiation transmitted by the canopy

Rising N supply stimulated plant growth and thus GAI development. Peak values of GAI occurred in June and were similar between both

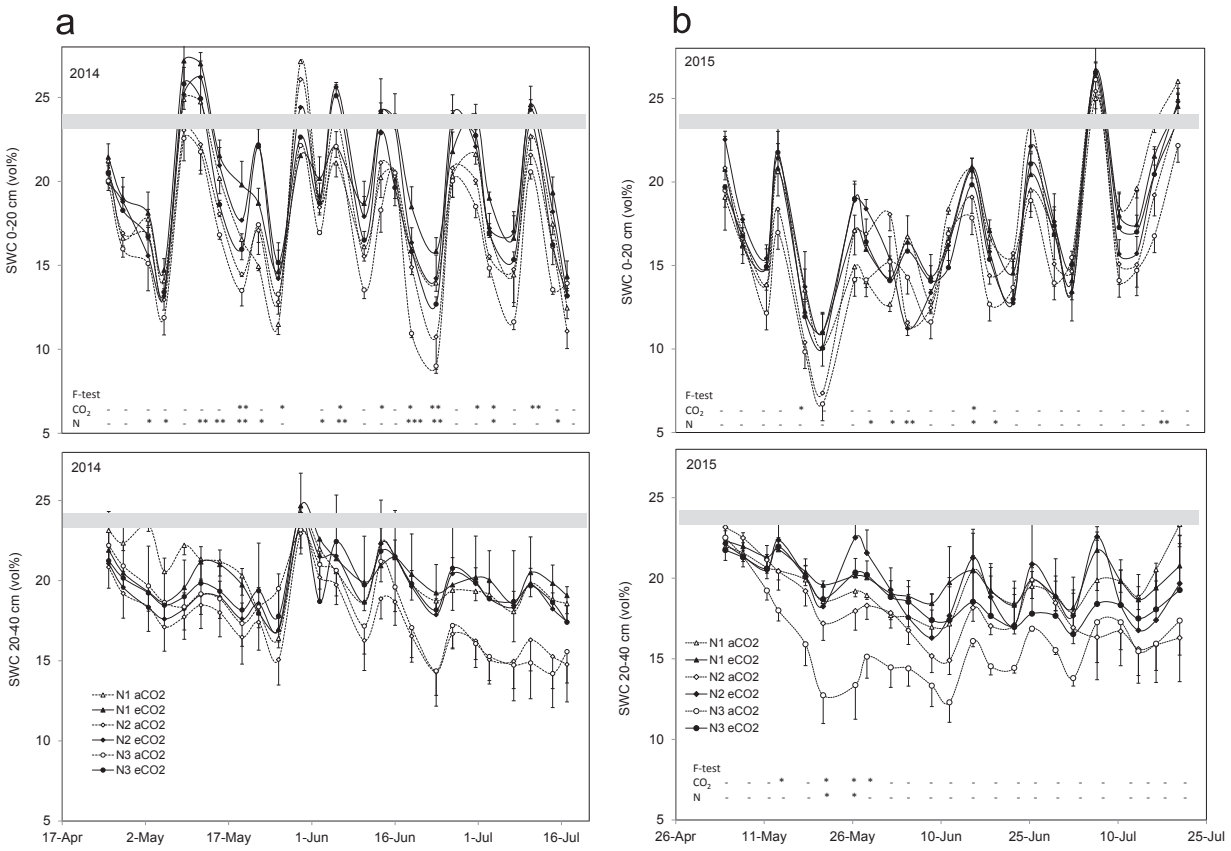

Fig. 3. Seasonal changes in volumetric soil water content (SWC) in the upper (0–20 cm depth) and lower layer (20–40 cm depth) of wheat grown in 2014 (a) and 2015 (b) with different levels of nitrogen (deficient, N1; adequate, N2; excessive, N3) and CO_2 supply ([aCO_2], [eCO_2]). Values are given with standard error (n = 3). The gray line shows SWC at field capacity. F-test results of the effects of nitrogen and CO_2 supply on SWC: $p < 0.05$, *; $p < 0.01$, **; $p < 0.001$, ***.

Table 3
Summary of seasonal evapotranspiration (ET) of wheat grown under different CO_2 ([aCO_2], [eCO_2]) and nitrogen supply (deficient, N1; adequate, N2; excessive, N3) during 2014 and 2015. ET was calculated from rainfall, irrigation (Irrig) and the changes in soil water content (dW) over the period (25th April–17th July in 2014, 4th May–20th July in 2015). Values are given as means with standard error in parentheses (n = 3).

year	CO2 level	N level	Rain (mm)	Irrig (mm)	dW (mm)	ET (mm)	CO_2 eff.
2014	[aCO_2]	N1	181	21	27 (3)	229 (3)	
	[eCO_2]	N1	181	21	20 (2)	222 (2)	−3%
	[aCO_2]	N2	181	101	31 (4)	313 (4)	
	[eCO_2]	N2	181	96	21 (3)	298 (3)	−5%
	[aCO_2]	N3	181	111	25 (1)	318 (1)	
	[eCO_2]	N3	181	96	22 (2)	300 (2)	−6%
2015	[aCO_2]	N1	122	121	−17 (2)	226 (2)	
	[eCO_2]	N1	122	106	−4 (10)	223 (10)	−1%
	[aCO_2]	N2	122	171	7 (4)	300 (4)	
	[eCO_2]	N2	122	141	0 (3)	263 (3)	−12%
	[aCO_2]	N3	122	208	5 (5)	334 (5)	
	[eCO_2]	N3	122	166	−3 (9)	284 (9)	−15%

years amounting to ca. 2.0, 4.5 and 5.5 $m^2\,m^{-2}$ under N1, N2 and N3, respectively. Consequently, the effect of N supply on GAI influenced radiation transmission to the soil surface (Fig. 4). It decreased until mid of June, when light transmission was about 20% under N1 and only about 5% under N2 and N3. The [eCO_2] effect on GAI development was relative low and did not influence radiation transmission to the soil surface. Later in the season the gradual increase of radiation transmission that was observed resulted from the fact that transmission was measured from the green fraction of the canopy, which decreased until grain maturity. However, transmission of the whole canopy rather may have remained unchanged from mid of June until maturity. Thus, the seasonal mean of radiation incident to the soil surface between stem elongation and maturity amounted to ca. 30%, 10% and 6% under N1, N2 and N3, respectively.

Table 4
F-test results for the effect of two CO_2 and three N treatments on evapotranspiration (ET), above ground biomass production (AGBM) and water use efficiency (WUE) in the 1st and 2nd experimental year. $p < 0.05$, *; $p < 0.01$, **; $p < 0.001$, ***; n.s., not significant.

Variable	year	CO_2	N	C× N
ET (mm)	2014	***	***	ns
	2015	***	***	**
AGBM (g m^{-2})	2014	*	***	ns
	2015	*	***	ns
WUE (g kg^{-1})	2014	**	***	ns
	2015	***	***	*

Table 5
F-test results for the effect of two CO_2, three N treatments and two years on evapotranspiration (ET), above ground biomass production (AGBM) and water use efficiency (WUE). $p < 0.05$, *; $p < 0.01$, **; $p < 0.001$, ***; n.s., not significant.

Variable	CO_2	N	year	C× N	C×Y	N×Y	C× N× Y
ET (mm)	***	***	**	**	*	***	n.s.
AGBM (g m^{-2})	**	***	n.s.	n.s.	n.s.	*	n.s.
WUE (g kg^{-1})	***	***	n.s.	**	n.s.	***	n.s.

Table 6
Summary of the effects over two years of different supply of N (deficient, N1; adequate, N2; excessive, N3) and of CO_2 ([aCO_2], [eCO_2]) on evapotranspiration (ET), above ground biomass production (AGBM) and water use efficiency (WUE) of wheat.

N level	ET (mm)			AGBM (g m^{-2})			WUE (g l^{-1})		
	[aCO_2]	[eCO_2]	% eff.	[aCO_2]	[eCO_2]	% eff.	[aCO_2]	[eCO_2]	% eff.
N1	227	223	−2	771	904	17	3.39	4.07	20
N2	307	280	−9	1473	1739	18	4.80	6.22	30
N3	326	292	−10	1569	1808	15	4.81	6.20	29

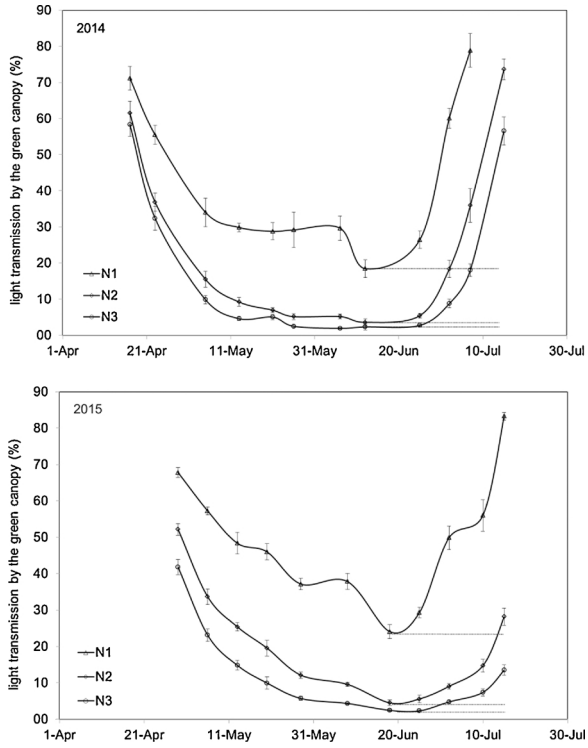

Fig. 4. Seasonal changes in light transmission by the green canopy of wheat grown over two years with different levels of nitrogen (deficient, N1; adequate, N2; excessive, N3) and averaged over the two CO_2 treatment levels. Values are given with standard error (n = 6). Dotted lines indicate transmission by the whole canopy during senescence (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

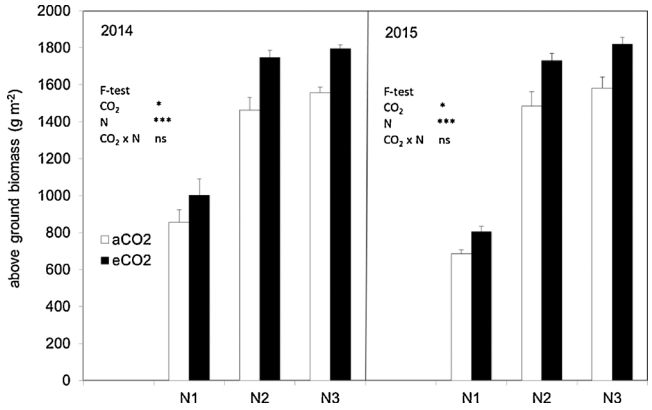

Fig. 5. Effect of different CO_2 ([aCO_2], [eCO_2]) and nitrogen supply (deficient, N1; adequate, N2; excessive, N3) on above ground biomass production between stem elongation and grain maturity in the 1st (2014) and 2nd (2015) experimental season. Values are given with standard error (n = 3).

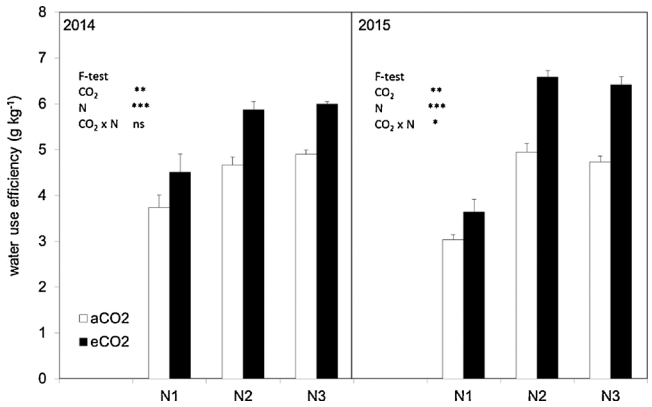

Fig. 6. Effect of different CO_2 ([aCO_2], [eCO_2]) and nitrogen supply (deficient, N1; adequate, N2; excessive, N3) on water use efficiency of above ground biomass production (WUE) between stem elongation and grain maturity in the 1st (2014) and 2nd (2015) experimental season. Values are given with standard error (n = 3).

3.4. Above ground biomass production and water use efficiency

N supply and CO_2 enrichment both significantly increased total above ground biomass produced from stem elongation until maturity (Table 4 and 5). Biomass was very similar between both years in the N2 and N3 treatments (Fig. 5), but was slightly higher in 2014 than in 2015 in the N1 treatment, which corresponds to the slight differences in fertilizer quantities used in 2014 (40 kg N ha^{-1}) and 2015 (35 kg N ha^{-1}). [eCO_2] significantly increased biomass production and across both years this effect was 17% under N1, 18% under N2 and 15% under N3 (Table 6).

Water use efficiency (WUE) was more varied among the different treatments in 2015 than in 2014 (Fig. 6). WUE strongly increased with N supply. In the 1st year, the [eCO_2] effect on WUE was slightly larger at the high N levels (+24%) than at N1 (+21%). In the 2nd year, the effect became even greater for the high N levels (+34%), while under N1 the [eCO_2] effect remained at 21%. Thus, there was a significant CO2 x N interaction on WUE only in 2015, but when data from both years were subjected to statistical analysis (Table 5), then there was still a significant CO2 x N but not CO2 x N x year interaction. Data averaged over both seasons indicate an increase of WUE of 21% under N1 and of 30% under N2 or N3 (Table 6).

4. Discussion and conclusions

The objective of the present study was to evaluate if and to what extent elevated CO_2 levels affect the water use of wheat plants under field conditions and whether this is influenced by the N nutrition. It is the first study, in which this question has been analysed for wheat grown under the temperate climate conditions of central Europe.The results obtained over two years indicate that [eCO_2] decreased ET significantly less under low N (−2%) than under high N (-10%). In addition, there were clear differences in the CO_2 response between years regarding the effect of CO_2 under high N supply. Plants grown under [eCO_2] and with high N (180–320 kg N ha^{-1}) required up till 6%

less water in the 1st year and 15% in the 2nd year. Our findings in 2014 correspond to the results of a previous two-year FACE study with wheat under warm arid climate conditions in Arizona (Hunsaker et al., 2000). In this study the CO_2 response of ET was quite similar between years and the decrease amounted to 1% and 4% under low and high N supply, respectively. However, FACE studies with other C3 crops grown under high N supply revealed also interannual fluctuation of the effect of [eCO_2] on ET varying from −9% up to −16% (Bernacchi et al., 2007; Magliulo et al., 2003). Thus, our multi-year mean of the FACE effect on wheat grown under high N (−10%) is in agreement to the −12% decrease of ET observed for potato and soybean (Bernacchi et al., 2007; Magliulo et al., 2003) and also very close to the values found for C4 crops (Conley et al., 2001; Hussain et al., 2013; Manderscheid et al., 2014). Accordingly, growth of C3 crops will benefit from rising CO_2 concentrations not only due to an increase of photosynthesis (Long et al., 2004; Kimball, 2016) but also due to a reduced water demand. However, climate change will also increase temperature and ozone levels, which are likely to have adverse effects on crop growth (Porter et al., 2014).

It is commonly agreed to that the decline of ET under [eCO_2] finally results from the decrease of stomatal conductance, which was found to be slightly more affected under low than high N supply (Li et al., 2004; Wall et al., 2000). While this effect reduces transpiration at the leaf level, in the long term [eCO_2] could increase leaf area resulting in an increase of transpiration at the whole plant level. However, leaf area index of wheat is only slightly affected by [eCO_2] as observed in the present and also in previous FACE experiments (Brooks et al., 2000; Weigel and Manderscheid, 2012). Measurements of sap flow of main stem tillers of wheat in the Arizona FACE showed that under ample N and water supply FACE decreased canopy transpiration on average by 15% (Senock et al., 1996). In our experiment this value should be about 18%, because of the difference in CO_2 enrichment levels used in the Arizona FACE and our FACE study. Given that under high N supply evaporation accounts for about 10–20% of ET in the period from stem elongation until grain maturity (Chen et al., 2010), a 18% decrease of whole plant transpiration without affecting evaporation would theoretically result in an ET decrease of 15%. This number corresponds to the maximum CO_2 response observed in the 2nd year of our study and also to the upper values found for soybean and potato (Bernacchi et al., 2007; Magliulo et al., 2003). In the low N treatment of our study, in which leaf area index did not exceed $2\,m^2\,m^{-2}$, evaporation may account about 40%–50% of ET (Wang et al., 2014). Consequently, ET should have been decreased only by about 10%, if FACE decreases canopy transpiration by 18% without affecting evaporation. However, in our and in the biennial study in Arizona (Hunsaker et al., 2000), the [eCO_2] induced decrease of ET under N deficiency was considerably lower (−1 to −2%) than −10%, suggesting an increase of evaporation by [eCO_2] under this N level.

Evaporation depends on the fraction of soil surface exposed to sunlight and surface soil moisture. The larger contribution of E to ET under low than high N results from the less dense canopy and the greater amount of light transmitted to the soil surface. In our study light transmission to the soil surface between stem elongation and maturity averaged 30% under low and < 10% under high N supply. This agrees to findings of a wheat study by Chen et al. (2010) where effects of row spacing on ET were investigated. [eCO_2] increases soil moisture primarily in the upper layer as shown here and in previous FACE studies with wheat (Burkart et al., 2011; Hunsaker et al., 2000) and other crop species (Gray et al., 2016; Magliulo et al., 2003; Manderscheid et al., 2014). Since E strongly depends on water content in the upper soil layer, it seems obvious that E is increased by [eCO_2]. Moreover, it can be assumed that the stimulation of E under [eCO_2] is greater under sparse canopies of wheat since more radiation energy is available at the soil surface for evaporation of the soil water. Slight increase of vapour pressure deficit of the canopy air under [eCO_2] as found in a previous study (Burkart et al., 2011) may have also increased evaporation.

The question remains of what are the reasons for the interannual variation of the CO_2 response of ET under high N supply as found here with winter wheat and in other FACE studies with soybean and potato (Bernacchi et al., 2007; Magliulo et al., 2003). Bernacchi et al. (2007) suggested that water availability over the season may have contributed to the variation between years. However, in our experiment water supply was strictly controlled and thus quite similar between both years. One important difference was that the crop water demand was covered mainly by rainfall in 2014 and by irrigation in 2015 due to the differences in precipitation between the two years. This involved that moisture content in the upper soil layer fluctuated stronger in the 1st as compared to the 2nd year. Because the [eCO_2] effect on soil moisture occurred more frequently in 2014 compared to 2015, it can be assumed that evaporation was stronger increased by [eCO_2] in 2014 than in 2015 and that this process may have contributed to the finding that the [eCO_2] effect on ET under high N supply was lower in 2014 (−6%) than in 2015 (−15%). In addition, results of ET in 2014 may have been confounded by deep drainage of water at the beginning of June when soil water content in 0–40 cm depth shortly exceeded field capacity. A rough assessment with the AMBAV model by the German weather service (Kersebaum et al., 2005) showed about 15 mm leachate for this time.

In the Arizona FACE experiment (Hunsaker et al., 2000), all different CO2 x N treatments received the same irrigation amount until grain filling, which occured in April. The only exception was that irrigation to the low N treatment was curtailed in May in both years due to accelerated maturity (Hunsaker et al., 2000). Given the decrease of canopy transpiration under FACE based on sap flow measurements (Senock et al., 1996), it is conceivable that this irrigation practice increased soil surface moisture and thus evaporation, weakening the effect of [eCO_2] on ET. This idea is supported by our results of 2015 that irrigation was reduced under [eCO_2] from booting to grain filling while there were hardly any differences in soil water content between the [aCO_2]and [eCO_2] plots. Hunsaker et al. (2000) found similar evaporation under [aCO_2] and [eCO_2] and only a slight difference of evaporation between N deficiency and high N supply. However, the evaporation rates calculated in their study were generally very low and thus also the percentage contribution of evaporation to ET. Moreover, our results are also in contrast to the outcome of a recent study with sixteen wheat simulation models (Cammarano et al., 2016), in which ET was predicted to be decreased only by 4% if [CO_2] rises from 360 ppm to 720 ppm. Moreover, it was found that transpiration was only slightly affected (-2%) and evaporation was not increased but rather decreased (−9%) under [eCO_2] (Cammarano et al., 2016).

In our study water use efficieny (WUE) was defined by biomass production per unit ET, whereas in the Arizona FACE study WUE was based on grain yield per unit ET (Hunsaker et al., 2000). Both studies indicated that [eCO_2] improved WUE stronger under high N than low N supply. However, in the Arizona FACE study the lower CO_2 response under N deficiency results from both a smaller effect on ET and grain yield (Hunsaker et al., 2000), whereas in our study the lower CO_2 effect under N deficiency was only from a smaller effect on ET.

In conclusion, our FACE study under temperate climate is consistent with the Arizona FACE study conducted under warm and arid climate (Hunsaker et al., 2000) that [eCO_2] increases soil moisture especially in the upper layer and decreases ET. The ET decrease, however, was only present for wheat with large canopies but vanished if canopies were sparse due to N deficiency. We tried to identify the reasons for the CO_2 x N interaction on water use and for the interannual variability of the CO_2 response under high N. For both cases, we argue that the variation of the CO_2 response of ET might be due to variation of the effect of [eCO_2] not on transpiration but on evaporation. It is argued that the increase of soil moisture in the upper layer under FACE can lead to an increase of evaporation. Moreover, this effect will be stronger under low than under high N since sunlight at the soil surface needed for evaporation is much higher under sparse than under dense canopies. These processes

finally seem to be responsible for the clear interaction of CO_2 and N supply on water use efficiency of biomass production, which can be increased up to 30% by + 200 ppm. Overall, the decrease of ET suggests that seasonal water use of well-fertilized wheat will improve under eCO_2 and this might be augmented by agricultural management reducing seasonal evaporation, for example subsurface irrigation, mulching or controlled deficit irrigation (Ali and Talukder, 2008).

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